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NEW DATA ON NORTH AMERICAN OAK FERNS, GYMNOCARPIUM

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The oak ferns, Gymnocarpium Newman, include few taxa. Except for one or more separate and endemic elements in eastern Asia (cf. Pichi-Sermolli, 1965. p. 148), there are only two basic species over most of the circumboreal range. Nevertheless, there are controversial points regarding both the generic treatment and the species taxonomy. The common oak fern, Gymnocarpium dryopteris (L.) Newman has broadly triangular leaf blades with the axes so sparsely glandular that they are usually designated as "glabrous." The "limestone" oak fern, G. robertianum (Hoffm.) Newman, is far rarer and more sporadic in most of its range. It has narrower leaf blades, and the blade axes (and the lamina) are densely glandular. Both of these ferns are variable, both in habitat and morphology. Dwarfed plants of G. robertianum, especially those growing on dryish rock cliffs, may tend to mimic the leaf outline of G. dryopteris. Fully developed, however, the characteristics of

¹Research supported by National Science Foundation Grant GB-2025. I wish to acknowledge the aid of Miss Sandra Smith and Mrs. Katherine Lim Chen, and the suggestions of Doctors E. T. Wherry, Eric Hultén, and Conrad V. Morton. The following herbaria kindly lent materials: Cranbrook Institute of Science, Gray Herbarium, Missouri Botanical Garden, U. S. National Museum, and the Naturhistoriska Riksmuseet, Stockholm. Dr. J. H. Soper made it possible for me to study the oak ferns in the herbarium at the University of Toronto.



PLATE 1328

Fig. 1. Gymnocarpium dryopteris var. disjunctum. Voucher specimen, n=40, Wagner 63087 and Kruckeberg (MICH).

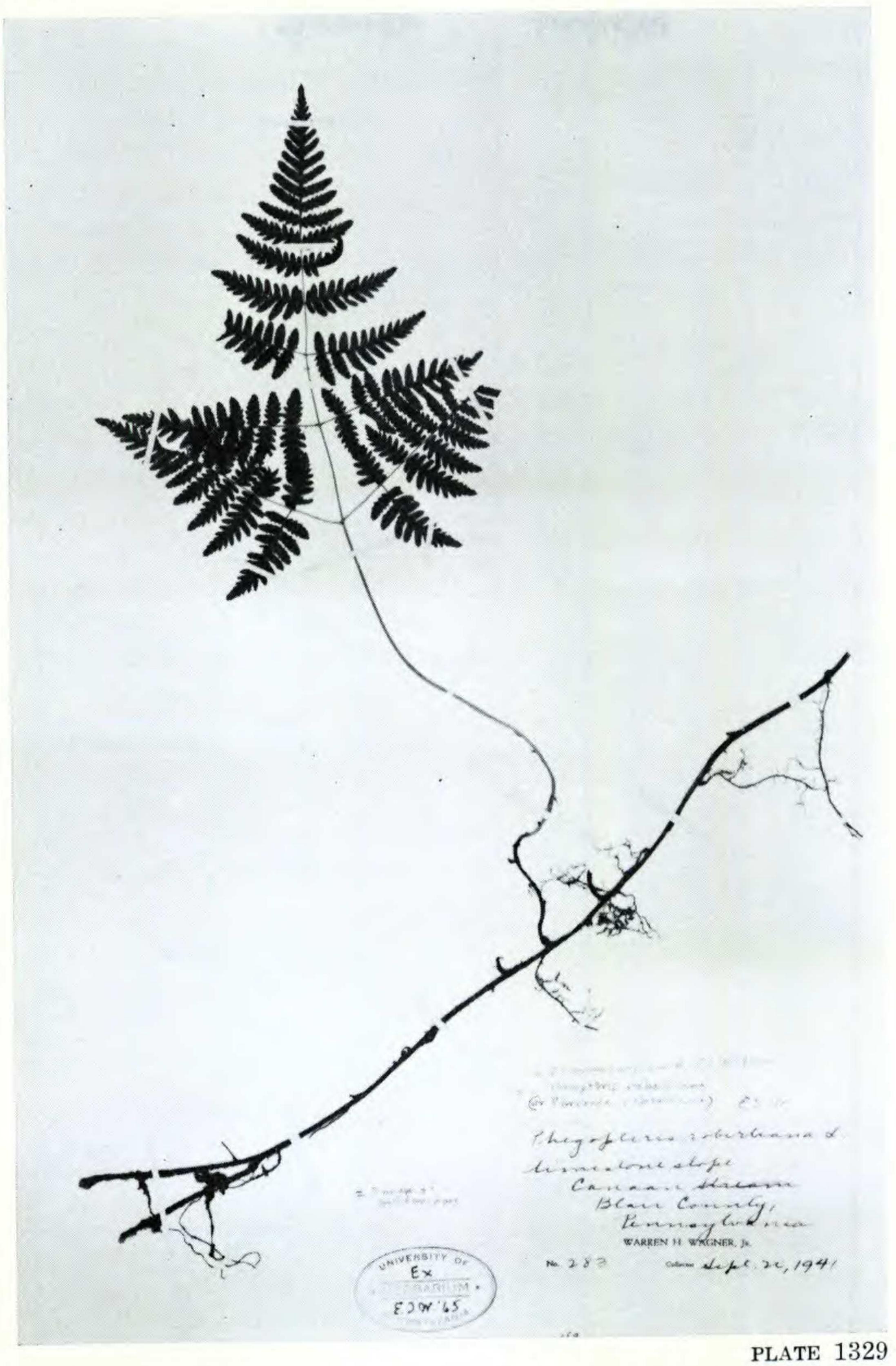


Fig. 2. Gymnocarpium heterosporum n. sp. Type specimen. Wagner 283 (MICH).

these plants are distinctive and most authors have upheld them as separate species. Good keys and brief descriptions are found in familiar manuals and guides (e.g., Tutin et al., 1964; Wherry, 1961); and the taxonomic characters are fairly well established.

At least two recent writers (Lawalrée, 1950; and Boivin, 1962) have questioned whether the two widespread taxa are specifically different. This question will be discussed further below. Also, there has been some disagreement about the generic placement of the oak ferns, but this matter will not be dealt with. Suffice it to say, the combination of characters does seem very well-marked, and in the past few years there has developed a widespread tendency to recognize Gymnocarpium as a distinct genus. The question is what its relationships are. The base number of x = 40 is quite different from such thelypteroid ferns as Phegopteris (x = 30), Cyclosorus (x = 36), and such species of Thelypteris as T. palustris (x = 35) and T.

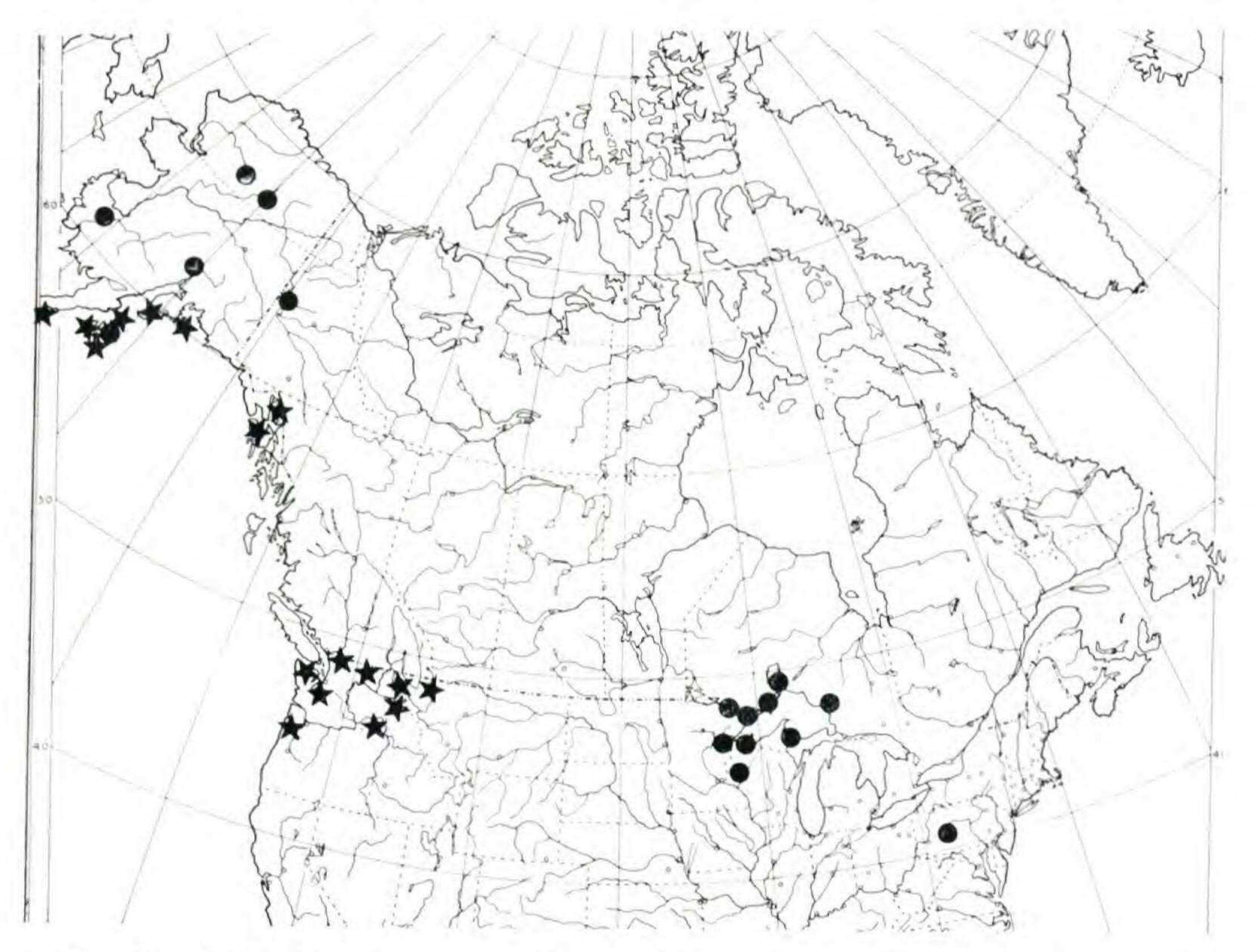


Fig. 3. Distribution map. Stars = very small spored G. dryopteris (less than 23.9×1.18 microns). Dots = G. heterosporum.

noveboracensis (x = 27). The chromosome number of Gymnocarpium resembles that of typical aspidioid ferns (e.g., Dryopteris, Cystopteris, Polystichum, Tectaria, Ctenitis, etc.) with x = 40, 41, or 42.

Elizabeth Root (1961) studied intermediates between G. dryopteris and G. robertianum and pointed out, for the first time, that "the majority of the spores of all intermediate specimens were found to be abortive." Since her study we have learned that the "hybrid" Gymnocarpium is much more frequent and widespread than had been heretofore realized, as is illustrated in the map (Fig. 3, dots). We have also discovered that there are three ploidal levels present in North American Gymnocarpium — the diploid, triploid, and tetraploid. These facts will be examined below in connection with the following questions: Are G. dryopteris and G. robertianum distinct species? Should the western representative of G. dryopteris be recognized as a separate variety or subspecies? What is the nature of the plants which are morphologically intermediate between G. dryopteris and G. robertianum?

THE DISTINCTNESS OF G. DRYOPTERIS AND G. ROBERTIANUM

Boivin (op. cit.) is the most recent worker who endeavored to interpret taxon robertianum as merely a variety of G. dryopteris. He did not find it possible to uphold taxon robertianum as a species because "Tous les caractères donnés chevauchent largement, sauf celui de la glandulosité qui est assez net si l'on excepte 6 ou 8 spécimens (sur environ 200 examiné). Cette glandulosité est si fine et ces deux espèces sont si semblables que, sur une cinquantaine de spécimens glanduleux examinés, un bon quart étaient mésidentifiés." I should point out that herbarium collections of ferns are often misidentified. The fact that certain species (e.g., in Gymnocarpium, Dryopteris, and Botrychium) are commonly misidentified should not be used as a basis for taxonomic judgments.

The reasons for upholding G. robertianum as a distinct species, rather than a variety of G. dryopteris, fall into two

classes: (1) The morphology of well-developed specimens is unquestionably distinct, including characters of the overall blade outline, the details of segment form, and the glandularity. Small, ecologically depauperated or juvenile, specimens may of course cause difficulties if only gross characters are used. But the glandularity of G. robertianum is evidently always a dependable character. (Some of the problems of detecting the extent of glandularity in these plants could be alleviated by eliminating the unfortunate herbarium practice of pasting down fronds, thus coating the delicate glands with a thin "varnish" which makes them practically invisible.) The only really intermediate plants in respect to glandularity are those to be discussed below, but these plants are intermediate in other respects also between G. dryopteris and G. robertianum and they are probably of hybrid origin. (2) The second reason for upholding G. robertianum is simply the behavior of the natural populations. The two species grow together in numerous localities in the Great Lakes area, in exactly the same habitats and growth conditions, and their distinctness is immediately evident to the field worker. The fact that these two taxa can exist together sympatrically without merging, and the fact that there is no genomic difference (both have n = 80 in this region) in ploidal level, shows that using the varietal rank to express their relationships would be stretching that category too far (cf. Wagner, 1960). The differences between these ferns are best seen in the rich, shady swamps of northern Michigan where they develop to the maximum size in the luxuriant, moist conditions. Mixed populations are well known in several localities near the University of Michigan Biological Station (Cheboygan, and nearby Presque Isle Cos., Michigan).

GYMNOCARPIUM DRYOPTERIS VAR. DISJUNCTUM

The western North American representatives of *G. dry-opteris*, especially in Idaho, Oregon, Washington, U.S.A. and British Columbia, Canada, tend to develop unusually large fronds. The area is roughly that shown by the stars

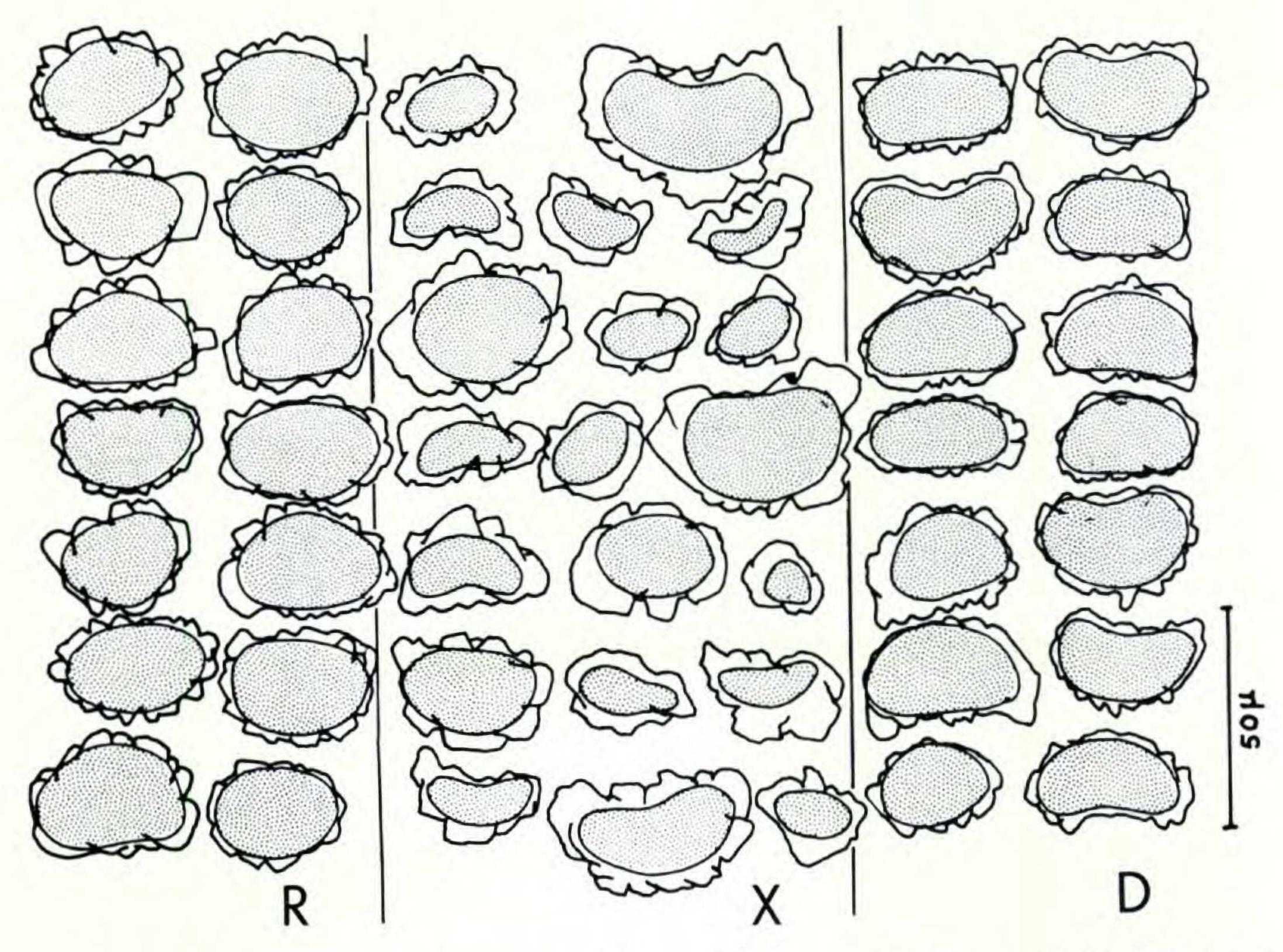


Fig. 4. Tracings of spores. Inner line = exospore; outer line = perispore. R. Gymnocarpium robertianum, Mich., Voss 4709 (MICH). X. G. heterosporum, Pennsylvania, Darling in 1956 (MICH). D. G. dryopteris, Mich., Voss 4708 (MICH).

of especially small-spored plants in Figure 3. In the most extreme form these plants become thrice-pinnate and the larger segments are more toothed than in typical G. dryopteris. Under the guidance of Dr. Arthur R. Kruckeberg of the University of Washington, I had an opportunity to study this form in the field. The best plants (Fig. 1) were seen in the deep coniferous woods at Denny Creek turnoff along U.S. 10, in the Snoqualmie National Forest, King Co., Washington. Here the "giant" G. dryopteris flourishes in damp, mossy forest with such other ferns as Dryopteris dilatata and Athyrium filix-femina, the latter two species also becoming remarkably large. Chromosome materials were obtained and squashes of meiosis showed clearly n = 40 pairs (Figs. 6 and 7, top illustrations). This is the first discovery of the diploid condition in the genus Gymnocarpium, all previous counts for which indicated the tetra-

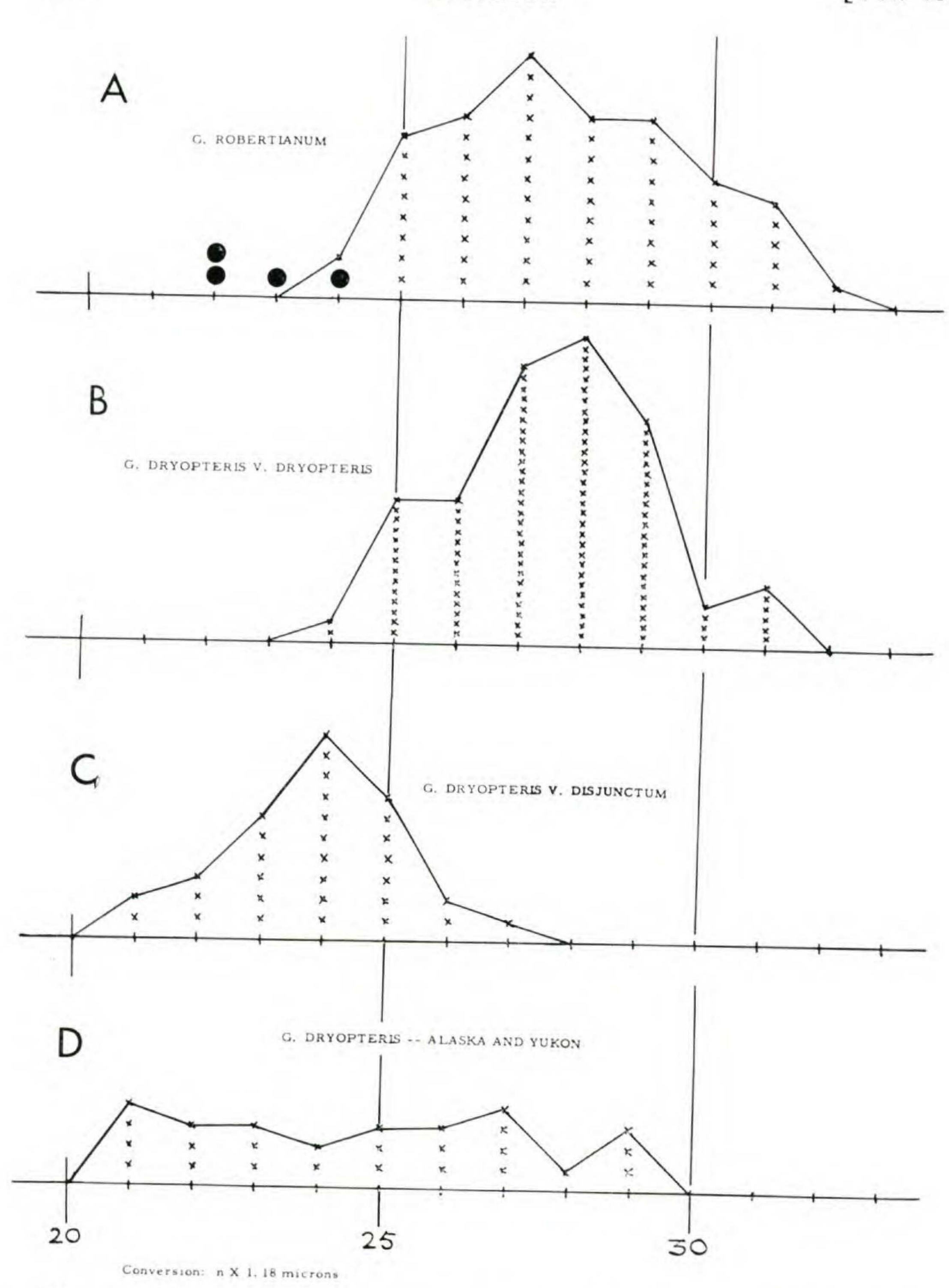


Fig. 5. Frequency histograms of spore lengths (exospore only). Each cross equals a 10-spore sample from a separate collection (Dots = spore samples of G. continentale). A. G. robertianum, all collections. B. G. dryopteris, all collections from Colorado east to Europe. C. G. dryopteris, all collections from British Columbia and Oregon east to Alberta and Montana. D. G. dryopteris, all collections from Alaska and Yukon. (Conversion: n × 1.18 microns).

ploid condition of n=80. (According to spore size, as shown in Fig. 5, A, the chromosome number of the Siberian G. continentale may also turn out to be diploid.)

For several reasons — the diploid chromosome number, the smaller spores (Fig. 5), the larger, more divided leaf (Fig. 1) and the distinctive western range — I choose (with some reluctance, however) to uphold the plants with this combination of characters as a separate variety. Morton (1941, p. 217) pointed out that the name disjunctum was based upon specimens from Sitka, Alaska, "and refers to certain large, lax forms that are essentially tripinnate, with the lower tertiary pinnules somewhat spaced out." At the time of his writing, Morton was of the opinion that "they do not seem to be worth nomenclatural recognition . . ." Boivin (op. cit.), on the contrary, upheld the large form as a distinct variety.

Although I am inclined to agree now that var. disjunctum (Led.) Ching should probably merit recognition, I must point out that the situation becomes very complicated in Alaska and the Yukon, where both small- and large-spored types occur in the same general area (note the frequency histograms in Fig. 5, D). In this region also, we find numerous dwarfed individuals of both types, so that the gross appearance typical of "var. disjunctum" becomes modified and indistinguishable in many specimens from "var. dryopteris," using the respective spore sizes as the criterion. Thus many specimens from the far northwest of North America cannot be readily identified. Dwarfing obscures the gross characters of the fronds; and the overlap of spore sizes between the diploid and tetraploid conditions is such that many specimens could not be identified without chromosome counts.

Our spore surveys have uncovered still other complications, the full meaning of which must await further study. It turned out that a number of collections of what I had interpreted to be ordinary "var. dryopteris" have abortive spores which in appearance match those of the presumed hybrid fern to be discussed below (like those in Fig. 4, \times).

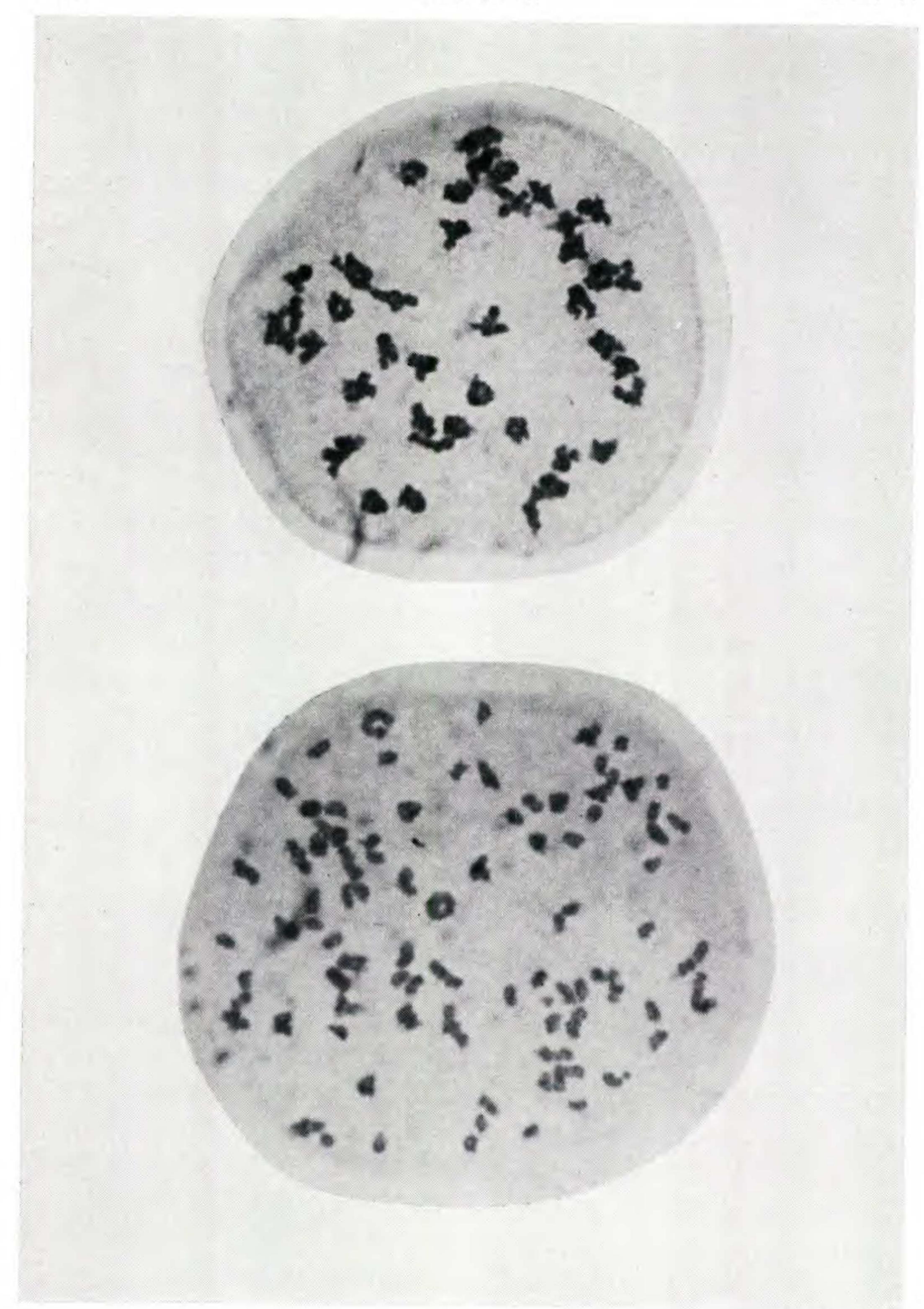


PLATE 1330

Fig. 6. New chromosome conditions in Gymnocarpium. Top: G. dryopteris var. disjunctum diploid, n = 40 pairs, $Wagner\ 63087$ and Kruckeberg (interpretation top left in Fig. 7). Bottom: G. heterosporum triploid, $3 \ x = c$. 120, Wherry s.n., from Blair Co., Pennsylvania, in 1956 (bottom left in Fig. 7).



Fig. 7. Camera lucida interpretations of chromosome squashes. Top: Diploids, same locality as in Fig. 6. Bottom: Triploids, same locality as bottom photograph in Fig. 6.

Miss Virginia M. Morzenti kindly examined these collections and confirmed that the morphology of the abortion is very similar in the "sterile" G. dryopteris and the putative cross, G. heterosporum. It seems possible that at least some of these collections may be apomictic derivatives of G. dryopteris var. disjunctum (the diploid) × var. dryopteris (the tetraploid), assuming here, as elsewhere in this discussion, that the type of var. disjunctum corresponds to the diploid, large-leaved western plant. We failed to find a single example of G. robertianum in all those that we studied which showed a similar abortion of spores. Thus, if one argued that these "sterile" G. dryopteris plants might represent mutations that are propagated locally by rhizomes, we wonder why similar mutations were not found in the related G. robertianum. Those collections we found of presumably "sterile" G. dryopteris will not be enumerated in detail here, but their geographical distribution is extremely wide as shown by the following records: Alaska (2 collections), Alberta (1), British Columbia (1), Wisconsin (1), Michigan (5), New York (4), Vermont (2), Maine (1), New Hampshire (1), Quebec (1), Newfoundland (2), and Nova Scotia (1). Further research on these curious "sterile" oak ferns with the morphology of *G. dryopteris* is greatly to be desired, especially to determine their cytological features and the mode of their reproduction.

THE APPARENT CROSS OF G. DRYOPTERIS AND G. ROBERTIANUM

This is the plant discussed by Root (op. cit.). As stated above, the apparent cross is much more frequent and widespread than we had previously realized. Its occurrence, especially in the western Great Lakes area, indicates that it is more than a rare hybrid, and I have concluded therefore that it should be given a binomial designation as an apomictic species, as follows:

Gymnocarpium heterosporum n. sp. W. H. Wagner. Planta frondis segmentique forma et glandularitate intermedia inter G. dryopteridem et G. robertianum; spori atro-brunnei, magnitudine et forma valde irregulares.

Type: Pennsylvania: Blair co., Canaan Station, limestone slope, W. H. Wagner 283 (transferred from University of Pennsylvania to Mich — 2 sheets, one fertile, the holotype (Fig. 2), and one sterile).

Representative Collections: U.S.A.: Pennsylvania: Blair co., 2 mi. n. w. of Hollidaysburg, among limestone rocks, T. Darling, Jr. in 1956 — same locality as the type (MICH). MICHIGAN: MARQUETTE CO., ca. 6 mi. n. w. of Ishpeming, near Ropes Gold Mine, n. w. 1/4 sect. 29, T 46 N. R 27 W, in woods on igneous rock cliffs, E. G. Voss 4707, W. H. Wagner and D. J. Hagenah 9415 (MICH). WISCONSIN: BAYFIELD co., Orienta Falls, G. H. Conklin and M. F. Somerville 1127 (WIS); BARRON Co., Barron Hills, just n. w. of Lehigh at the base of quartzite talus, N. C. Fasset 15817 (WIS), R. M. Tryon, Jr. 4154 (WIS, GH, MO). MINNESOTA: CARLTON CO., Carlton, Carlton-Thompson Gorge, St. Louis R., M. F. Somerville in 1928 (MICH); ST. LOUIS Co., observation tower at Ash River, Wagner 9034.5a (MICH); LAKE CO., Gooseberry Falls State Park, 15 mi. n. e. of Two Harbors, in crevice of diabase cliff, damp and shady, R. M. and A. F. Tryon, A. C. Faber 4889 (MO); 45 mi. n.e. of Two Harbors, Manitou Falls near Lake Superior, under ledge of diabase, damp and shady, R. M. and A. F. Tryon, A. C. Faber 4895 (MO). CANADA: ONTARIO. ALGOMA DISTRICT, rocky cliffs at edge of Soulier Lake, vicinity of Michipicoten Harbor, R. C. Rosie, H. M. Harrison, E. O. Hughes 1092 (TRT, GH). ONTARIO, THUNDER BAY DISTRICT, 1 mi. n. of Little Pigeon Bay, Crooks Twp., talus slope, mostly shale, common, C. E. Garten 1933 (TRT); ca. 19 mi. n. of Nipigon, spruce-fir thickets on damp moss-covered talus

at foot of cliff, E. G. Voss 10335 (MICH, TRT); 15 mi. e. of Port Arthur, 2 mi. w. of Silver Islet, shady sandstone talus, R. M. and A. F. Tryon, A. C. Faber 4963 (MO). U.S.A.: ALASKA: WISEMAN, on Middle Fork of the Koyukuk River, ca. 67° 30' N, 150° W, Edith Scamman 913

(GH).1

This fern, being intermediate between the two familiar species of Gymnocarpium, and having obviously peculiar spores might more appropriately be designated as merely a sporadic hybrid (e.g., as G. dryopteris \times robertianum). There are several reasons why this was not done. (1) The plants develop large colonies locally, and behave as an apomictic species. (2) As shown on the range map (Fig. 3) plants conforming to this description run from Alaska southeast through the western Great Lakes area (the region, evidently, of its greatest abundance) down to central Pennsylvania. (3) Cytogenetically (see below) at least one population, the type, is triploid, and not tetraploid as would be expected from our present knowledge of the parents as they occur in the eastern United States. The nearest diploids (judging from spore sizes and assuming correlation with the single diploid count) seem to be limited to the western part of the continent. (4) Finally, the intermediate is evidently to be found in at least some localities where one of the putative parents (G. robertianum) is unknown.

The holotype, but not the cotypes, of *Dryopteris linnaeana* C. Chr. f. glandulosa R. M. Tryon, Jr. (Amer. Fern Jour. 29: 5, 1939) is evidently the same as the plant described above. The author wrote of his new "form" that the "rachis varies in glandularity, some specimens having only a few glands, while others have relatively many and rarely the blade is slightly glandular." Judging from the specimens cited, the author included two kinds of populations — the form of G. dryopteris in which the glands are more frequent and conspicuous than usual, and the plant described above. As to the glandular form of G. dryopteris itself, I am not sure that it is worthy of recognition. In her survey (1961, p. 18) Mrs. Root concluded that "It is generally stated that

^{&#}x27;Additional collection localities not cited here but plotted in Fig. 3 were supplied by Dr. Eric Hultén.

the fronds and rachises of *G. dryopteris* range from glabrous to rarely slightly glandular. However, upon close examination of specimens from various localities it was found that *every* individual of this species examined has glands." In synonymizing "forma *glandulosa*" with *G. robertianum* (as "*G. dryopteris* var. *pumilum* (DC) Boivin"), Boivin (1962) was in error. Neither the type nor the cotypes of Tryon's form conform to the characters of *G. robertianum*.

Specimens of G. heterosporum in herbaria have previously been determined as one or the other of the putative parents, but most commonly as "G. robertianum" or "G. dryopteris f. glandulosa." The recognition of G. heterosporum is usually fairly easy in herbarium material, so long as the specimens have ripe spores. These tend to be discharged and to lie around the axes of the frond, sticking to the sheet. If the spores appear blackish and strongly irregular in size and shape, this is an excellent diagnostic feature, in combination with the presence of the intermediate condition of glandularity. The spores can be seen even with a dissecting microscope or a high power hand lens; and once their appearance is learned it becomes easy to pick out other collections with the same spore conditions, so a compound microscope is unnecessary. The spores of typical specimens of G. robertianum and G. dryopteris seem always to have a "glassy," tan or brownish color, and are strikingly regular. Both the soriferous specimens, as well as those which lack sori, of the intermediate oak fern will show the intermediate glandularity of the axes, especially on the upper parts of the rachis (if they have not been imbedded in herbarium paste). The glands of G. heterosporum are fewer and more widely spaced than they are in the densely glandular G. robertianum. In the field it is helpful to hold up the living fronds in the sun's rays and examine them with a good hand lens. The glands will glisten and thus be conspicuous, so that even small, sterile fronds of all three taxa, if growing together, may be separated.

Wherry (1942) described the habitat of the type population as follows (italics mine): "... the base of a steep

northwest-facing wooded slope, above a brook, the underlying rock being limestone which breaks into small angular blocks, from the crevices of which moisture oozes out, and by evaporation keeps the rocks cool." The Michigan station near Ishpeming, Marquette Co., is on steep shaded rock cliffs. In the latter area, the rocks contain serpentine. Garten took his specimens on a talus slope comprising mostly shale. The Lake Co., Minnesota, material was recorded from crevices of a "diabase cliff," while that from Barron Co., Wisconsin, came from "quartzite talus." The specimens from east of Port Arthur, Ontario, were found on "shady sandstone talus." Thus, ecologically, the substratum itself does not seem to matter much. The constant features of the habitats of G. heterosporum seem to be (a) shadiness, (b) moisture and humidity, (c) presence of rock substratum of some kind, the plants growing either directly from crevices of cliffs or upon the fallen talus. One or both of the presumed parental species may be present at the same locality.

CHROMOSOMES AND SPORES

The chromosomes and spores seem to have significance in this group of plants because of their variability and their correlation with each other and with other systematic data such as distribution and morphology of the fronds. There are three chromosome conditions. The tetraploid with n=80 or near that number is characteristic of G. robertianum as found by Manton and myself (Chiarugi, 1960; Fabbri, 1963). Judging from spore sizes (see Fig. 5) all populations of G. robertianum are probably tetraploid and the curve is normal. In Siberia, however, the rather similar G. continentale (Petrov) Pojark, has small spores (indicated by dots in the graph) and may be a diploid.

For G. dryopteris we first plotted all spore size averages and produced a broad, apparently undifferentiated curve. However, when we selected specimens from the area of presumably typical var. disjunctum (where we know there are diploids) an entirely different curve separated out. This area extends from British Columbia and Oregon east to

Alberta and Montana, and the spore sizes average between $23-25 \times 1.18$ microns¹ (Fig. 5, C) in maximum exospore diameter, in contrast to between $27-29 \times 1.18$ microns for var. dryopteris east of Colorado and including Europe (Fig. 5, B). Thus in G. dryopteris there is a correlation between spore size and polyploidy, as has been found in a number of other fern groups.

The "sterile-spored" *G. dryopteris* commented upon above may represent triploid populations, derived by interploidal hybridization and spreading by some means of spore disseminule not yet fully understood. The question is where the diploid and tetraploid may meet geographically. The graph of spore samples from Alaska (Fig. 5, D) shows values all the way from 21 to 29 micrometer units, strongly indicating that in this area, *G. dryopteris* is a mixture of ploidal levels.

It was extremely interesting to find that the type population of G. heterosporum (lower illustrations in Figs. 6 and 7) is triploid. Even though the pairing is very irregular, by totaling the estimated bivalents and univalents respectively of four sporocytes the following numbers resulted: (29) + 63, (33) + 50, (33) + 55, and (39) + 42. Their average was (33.5) + 52.5, or 119.5 chromosomes in all. Assuming that G. heterosporum is truly of hybrid origin and that both G. dryopteris and G. robertianum in the eastern U. S. are tetraploid, then it is possible that the type population originated as 2x G. dryopteris var. disjunctum \times 4x G. robertianum. Further cytological surveys of G. heterosporum in other areas are highly desirable. It is possible that 4x forms of it exist.

I must alert collectors to the need of obtaining fertile materials of these plants of which the sori contain ripe spores. Out of 500 specimens that we examined, 150 proved to be sterile or too young for spore observations. Also, I should point out that it is not correct that the spores of

¹Conversion factor: one micrometer unit = 1.18 microns. Fig. 5 is plotted in micrometer units only, from spores taken from herbarium specimens and mounted directly in diaphane.

Gymnocarpium lack perispores. Ching's description of "spores bilateral, warty, and without perispore" (quoted in Morton, 1941) surely does not conform to our observations. As shown in the spore tracings in Figure 4, there are two clearly defined layers — the outer, perisporial covering which is irregular, and the inner, exosporial boundary which is smooth. This is not different from other members of this group of ferns associated with Thelypteris and Dryopteris. The perispores of Gymnocarpium show up especially well in the abortive spores of "sterile G. dryopteris" and of G. heterosporum, where they actually are more or less exaggerated in development. This excessive perisporial thickness is probably the factor which produces the darker, nearly black, appearance of the spores as seen en masse.

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LACTUCA MURALIS IN NEW ENGLAND

Recently a number of duplicates from a collection of New Hampshire plants by Andrew P. Nelson, Assistant Professor of Biology at Dartmouth College, were sent to Professor Albion R. Hodgdon at the University of New Hampshire. Among these was a specimen of Lactuca muralis (L.) Gaertn. (A. P. Nelson 1059) that was collected by the side of a gravel road between Cornish Mills and Plainfield in the town of Cornish, Sullivan County, N. H. on August 6, 1964. Professor Hodgdon states that this is the first report for this species in New England. Gray's Manual, 8th edition, describes the species as growing on roadsides and in waste places, local, w. Que., and e. N. Y. to Mich. (Adv. from Eu.). In Gleason and Cronquist Manual of Vascular Plants (1963) it is listed as a native of n. Eu. now known from N. Y. and Que. Voucher specimens have been deposited in the herbarium of the New England Botanical Club, Cambridge, Mass. and in the Pringle Herbarium at the University of Vermont in addition to the specimens in the University of New Hampshire Herbarium and the Jesup Herbarium.

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